

MYCOTAXON

<http://dx.doi.org/10.5248/118.1>

Volume 118, pp. 1–15

October–December 2011

New records of *Geastrum* from Japanese sand dunes

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ABSTRACT— Basidiomata of three earthstars —*Geastrum campestre*, *G. corollinum*, *G. hungaricum*— were collected from sand dunes of the Japanese coasts. Those arenicolous fungi are newly recorded for Japanese mycobiota. Descriptions, comments and illustrations of basidiomata of the three fungi are provided.

KEY WORDS— biogeography, coastal environment, gasteromycetes, *Geastrales*, taxonomy

Introduction

The genus *Geastrum* Pers. belongs to *Geastrales*, *Phallomycetidae* (Hosaka et al. 2006) and includes currently about 50 taxa (Kirk et al. 2008). Most species of the genus are known as saprobes and are distributed throughout all continents except Antarctica. Several authors have systematically revised *Geastrum* (Staněk 1958, Ponce de Leon 1968, Dörfelt & Müller-Uri 1984, Dörfelt & Heklau 1987, Sunhede 1989). Several species have been recorded from multiple continents, although their taxonomic identities are doubtful because there are only a few molecular phylogenetic studies. Our preliminary morphological and phylogeographical analyses of the globally distributed “*G. triplex* Jungh.” indicate that the name represents an aggregation of multiple species (Kasuya et al. 2011a). This suggests the possible existence of many cryptic species in the genus.

Although 18 *Geastrum* species have hitherto been recognized from Japan (Imai 1936, Kawamura 1954, Ito 1959, Yoshimi & Hongo 1989, Sakamoto & Kasuya 2008, Kasuya et al. 2009, 2011b), comprehensive taxonomical and biogeographical studies of the genus have not yet been conducted. Therefore, to clarify the geographical distribution, morphological variations, and phylogenetic positions of Japanese *Geastrum*, we conducted morphological and molecular phylogenetic analysis of the genus based on the materials from multiple localities including Japan and other continents (Kasuya et al. 2011a).

Several *Geastrum* species favor semiarid to arid environments, e.g., well-drained sandy soils of coasts, deserts, and inland steppes. During our recent floristic and taxonomic investigations of Japanese *Geastrum* (Sakamoto & Kasuya 2008, Kasuya et al. 2009, 2011b), we recorded *G. kotlabae* V.J. Staněk, *G. minimum* Schwein., and *G. quadrifidum* Pers. from coastal sand dunes of Hokkaido and Honshu.

Some noteworthy *Geastrum* collections obtained by further fieldwork conducted in sand dunes along the Japanese coasts include *G. campestre*, *G. corollinum*, and *G. hungaricum*, which represent new distributional records for Japan. We describe the Japanese collections of these three species with the aid of illustrations showing morphological characters. We also compare them with related taxa and discuss the biogeographical and ecological features of the species.

Materials & methods

Fieldwork was carried out from September 2003 to October 2010 at three sites in coastal sand dunes of Hokkaido and Honshu, Japan: (1) Minehama, Shari, Hokkaido (43°55'34"N, 144°46'18"E); (2) Hitachi Kaihin Park, Hitachinaka, Ibaraki (36°23'54"N, 140°36'24"E); and (3) Fukude, Iwata, Shizuoka (34°39'51"N, 137°53'22"E). These sites well preserve coastal vegetation dominated by poaceous and cyperaceous plants. For morphological comparisons, we examined one additional *G. corollinum* specimen collected from an inland area of Honshu.

The examined specimens are deposited in the mycological herbarium of the National Museum of Nature and Science, Tsukuba, Ibaraki, Japan (TNS). Macroscopic characters were described from dried and fresh material. For light microscopic observations, freehand sections of the specimens were mounted in water, 3% (w/v) KOH, and 30% ethanol solution on glass slides. Forty randomly selected basidiospores were measured under a light microscope at 1000× magnification. Length measurements excluded the apiculus; average dimensions ± standard deviations are shown in brackets. The surface features of basidiospores were also observed by scanning electron microscopy (SEM). For SEM, a small portion of the gleba was dusted onto double-sided adhesive tape on a specimen holder, coated with platinum-palladium using an E-1030 Ion Sputter Coater (Hitachi, Tokyo, Japan), and examined with a S-4200 SEM (Hitachi, Tokyo, Japan) operating at 20 kV.

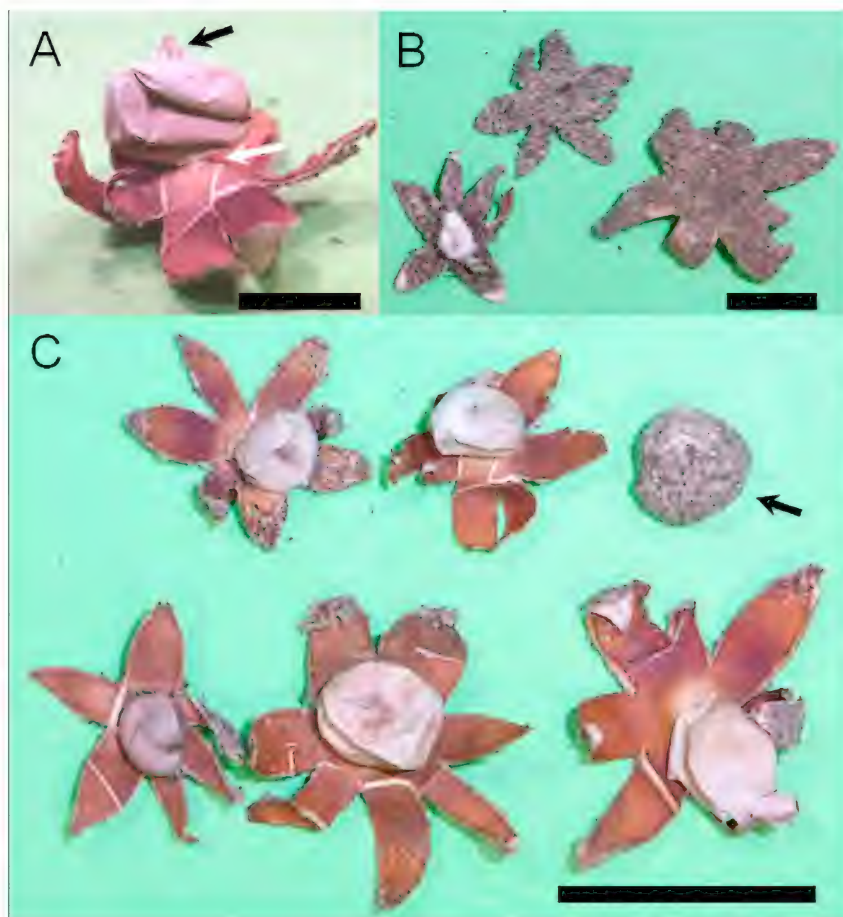


FIGURE 1. *Geastrum campestre*: macrocharacters (TNS-F-38710). A: Detailed structure of expanded basidiomata. Note plicate peristome (black arrow) and short stalk (white arrow). B: The mycelial layer of expanded basidiomata. C: Expanded and an unexpanded (arrow) basidiomata. Scale bars = 20 mm.

Taxonomy

Geastrum campestre Morgan, Amer. Nat. 21: 1027, 1887, as “*Geaster campestre*”.

FIGS. 1–2

JAPANESE NAME: Hamabe-no-hida-tsuchigaki (coastal dune’s plicate earthstar, newly named here).

UNEXPANDED BASIDIOMATA hypogeous to subhypogeous, depressed globose, globose to subglobose when young, ca. 5–12 mm diam., surface encrusted

with sand, whitish to slightly cineraceous. EXPANDED BASIDIOMATA 8–32 mm across when dried, 15–37 mm across when wetted, exoperidium splitting into 6–8 rays, weakly to strongly hygroscopic, rays arched with straight to slightly recurved tips in fresh state or when wetted, then partly or entirely covering the endoperidial body when old or dried. MYCELIAL LAYER thin, whitish, encrusted with sand and plant debris, persistent, attached to the fibrous layer for a long time and without forming basal remnants attached to the basidiomata. FIBROUS LAYER outer side almost completely covered with the mycelial layer, whitish to grey. PSEUDOPARENCHYMATOUS LAYER persistent, pale beige in fresh state, later becoming beige, reddish brown to dark brown. ENDOPERIDIAL BODY stalked, depressed globose, globose to subglobose, 3–11 mm diam., with or without apophysis. ENDOPERIDIUM pale brown, greyish brown to dark brown, finely pruinose or almost smooth when old, but usually distinctly pruinose or tomentose with whitish to beige crystalline material in fresh basidiomata, with an indistinct circular area surrounding the peristome. PERISTOME strongly plicate with 13–22 folds, almost concolorous or somewhat darker than endoperidium, broadly conical to mammiform, distinctly delimited, 1–2.5 mm long. STALK short but distinct, 0.5–1 mm long. COLUMELLA globose, ovoid to club-shaped in mature state, persistent, distinct. MATURE GLEBA olivaceous brown to brown.

MYCELIAL LAYER consisting of dimorphic hyphae: (I) 2–5 μm thick, hyaline, thick-walled, rarely branched; (II) 1.5–3.5 μm thick, hyaline, thin-walled, with clamp-connections, rarely branched. FIBROUS LAYER consisting of 2.5–6.5 μm thick, hyaline, thick-walled hyphae. PSEUDOPARENCHYMATOUS LAYER consisting of hyaline, yellowish brown to pale brown, thick-walled, almost bladder-like but variously shaped cells. ENDOPERIDIUM consisting of dimorphic hyphae: (I) 3.5–4.5 μm thick, yellowish brown, brown to dark brown, thick-walled, rarely dichotomously branched; (II) 2–4.5 μm thick, hyaline to pale yellowish brown, thin-walled, branched. HYPHAE OF THE COLUMELLA 2–6.5 μm thick, hyaline, pale yellowish brown to pale brown, thick-walled, rarely dichotomously branched. HYPHAE OF THE CAPILLITIUM hyaline to yellowish brown, thick-walled, 2–8 μm thick, tapered gradually towards subacute tips, dichotomously branched, surface usually encrusted with numerous amorphous remnants or crystalline materials but sometimes almost smooth. BASIDIA not seen. BASIDIOSPORES globose, densely verrucose, thick-walled, yellowish brown, 4.1–[4.9 $\pm$ 0.4]–5.7 μm diam. excluding ornaments, 5–[5.5 $\pm$ 0.3]–6.2 μm diam. including ornaments, verrucae conical to columnar-like, $\leq$ 0.8 μm high, with flat, rounded to subacute apexes, basal apiculus prominent.

HABITAT AND DISTRIBUTION: Uncommon in Japan, where it is gregarious on sand in coastal dunes in a warm-temperate zone near *Carex kobomugi*, *C. pumila*, and *Elymus mollis*. Several fresh basidiomata were collected in

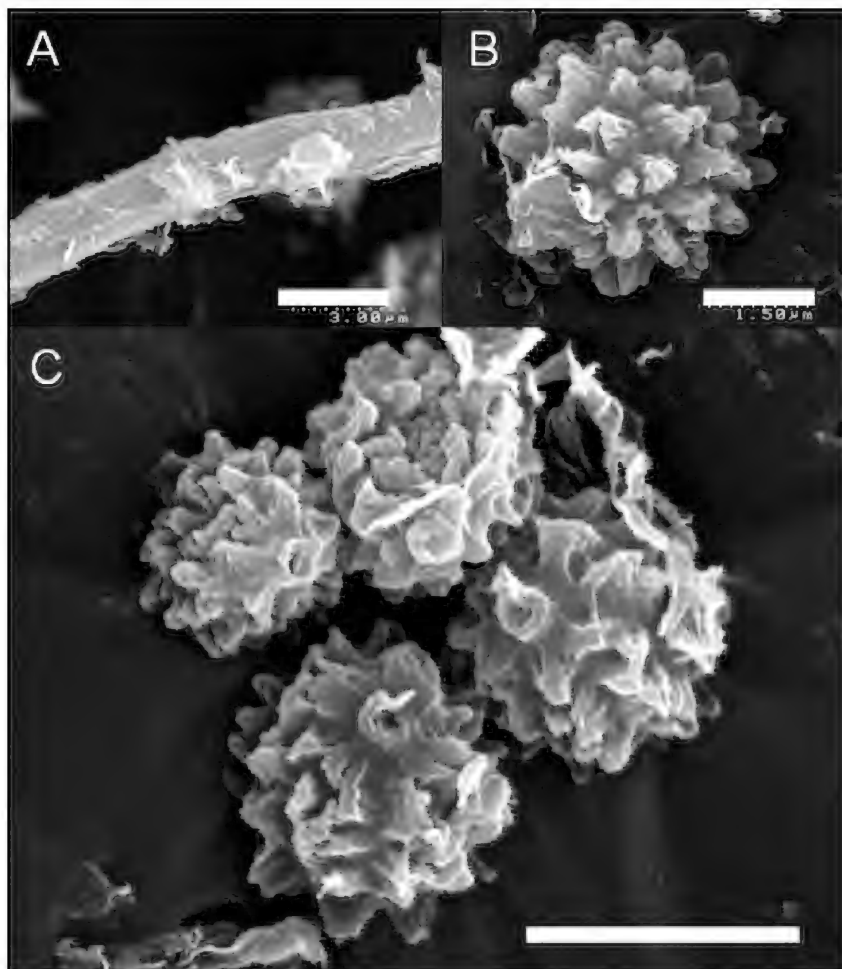


FIGURE 2. *Geastrum campestre*: SEM micrographs (TNS-F-38710). A: Hypha of the capillitium encrusted with amorphous remnants and crystalline materials. B: A basidiospore covered with dense verrucae. C: Basidiospores with prominent apiculus. Scale bars: A = 3 μm ; B = 1.5 μm ; C = 2 μm .

September. Known from Japan (Ibaraki, new record), Europe (Sunhede 1989), South Africa (Smith 1935), North America (Long & Stouffer 1948), Central America (Esqueda et al. 2003), Hawaii (Gilbertson et al. 2001), and Australia (Cunningham 1944).

SPECIMENS EXAMINED: JAPAN. IBARAKI PREFECTURE: Hitachinaka-shi, Nagasuna, Hitachi Kaihin Park: September 26, 2004, H. Sakamoto, TNS-F-38710.

COMMENTS: *Geastrum campestre* is well characterized by hygroscopic exoperidial rays, a mycelial layer encrusted with sand or debris, a stalked endoperidial body, and a distinctly delimited, plicate peristome. The morphology of the Japanese specimens agrees well with previous descriptions of *G. campestre* (Cunningham 1944, Long & Stouffer 1948, Sunhede 1989). However, the expanded Japanese basidiomata are usually smaller (≤ 37 mm wide when wet) than European specimens (≤ 65 mm wide, Sunhede 1989).

Geastrum kotlabae and *G. pouzarii* V.J. Staněk are morphologically and ecologically very similar to *G. campestre*. All three species have hygroscopic exoperidial rays and plicate peristomes and share similar habitats such as well-drained, sandy soil. However, the endoperidial body of *G. kotlabae* is completely sessile (Sunhede 1989, Sakamoto & Kasuya 2008). Basidiospores of *G. pouzarii* are larger (5.5–7 μm diam. including ornaments, Sunhede 1989) than those of *G. campestre*. Moreover, the mycelial layer of both *G. kotlabae* and *G. pouzarii* easily peels off at basidiome expansion (Sunhede 1989, Esqueda et al. 2003) whereas that of *G. campestre* remains attached to the fibrous layer for a long time. *Geastrum berkeleyi* Massee, which also produces stalked endoperidial bodies and plicate peristomes, clearly differs from *G. campestre* by its non-hygroscopic, much larger basidiomata (Kasuya et al. 2009).

Japanese material of *G. campestre* has been collected from sand dunes along the Pacific Ocean coast in the warm-temperate area of Eastern Honshu. The type specimen of *G. campestre* was collected from Nebraska, U.S.A., where it grows on dry open grasslands or on litter under conifers or deciduous trees (Long & Stouffer 1948). European and Australian specimens have been obtained from well-drained, sandy soil near coasts (Cunningham 1944, Sunhede 1989), and the species has been recorded from tropical deciduous forests in Mexico (Esqueda et al. 2003) and dry mountain forests in Hawaii (Gilbertson et al. 2001). These facts suggest that *G. campestre* prefers dry, well-drained open land but can grow in a variety of environments.

Geastrum campestre is known from all continents except Antarctica and its habitats are diverse. As several morphological variations have been reported (Sunhede 1989), *G. campestre* as currently defined may be a species complex.

Geastrum corollinum (Batsch) Hollós, Gasterom. Ung.: 65, 1904, as “*Geaster corollinus*”.

FIGS. 3–4

JAPANESE NAME: Chijire-tsuechigaki (Curled earthstar, newly named here).

UNEXPANDED BASIDIOMATA usually epigeous, rarely subhypogeous, subglobose, ovoid to onion-shaped with an umbo, 6.5–13 mm wide, 14–17.5 mm high including apical umbo, surface almost smooth to minutely wrinkled and not encrusted with sand or plant debris, ochraceous to pale brown. EXPANDED BASIDIOMATA 10–24 mm across when dried, 16–28 mm across when wetted,

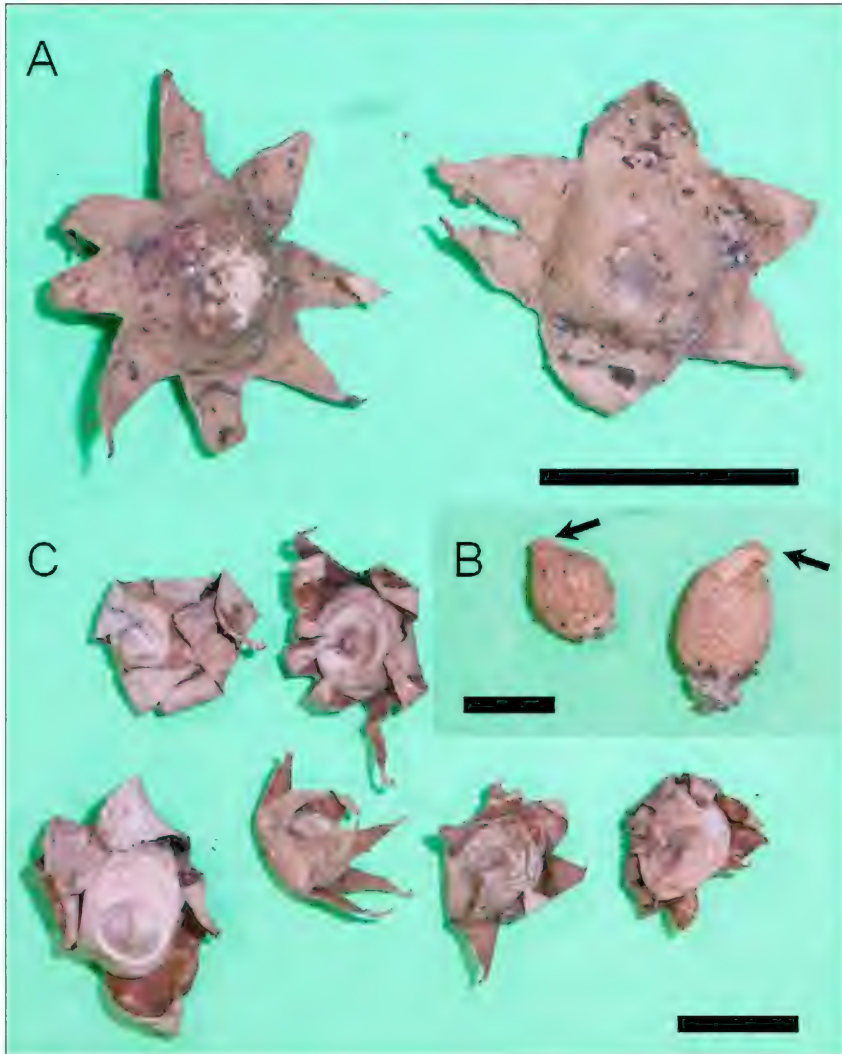


FIGURE 3. *Geastrum corollinum*: macrocharacters (TNS-F-38711). A: Two expanded basidiomata with distinctly delimited, fibrillose peristomes. B: Two unexpanded basidiomata with almost smooth surfaces. Note apical umbos (arrows). C: Expanded basidiomata showing hygroscopic exoperidial rays. Scale bars: A = 10 mm; B–C = 15 mm.

exoperidium splitting into 5–10 rays, hygroscopic, partly or entirely covering the endoperidial body and thus curled when dried, tips of the rays sometimes become recurved downwards in fresh state. MYCELIAL LAYER thin, yellowish

white, pale ochraceous to pale brown, smooth, without sand or plant debris, visible when unexpanded, but soon disappeared when basidiome expand. FIBROUS LAYER firm, persistently attached to the pseudoparenchymatous layer, outer side ochraceous to pale brown. PSEUDOPARENCHYMATOUS LAYER persistent, thin (>0.5 mm thick), pale beige in fresh state, later becoming ochraceous, reddish brown to dark brown, coriaceous when wetted or young, very hard when dried or old. ENDOPERIDIAL BODY sessile, depressed globose, globose to subglobose, 6–11.5 mm diam., without apophysis. ENDOPERIDIUM pale brown to greyish brown, almost smooth when old, but usually pruinose with whitish crystalline material in fresh or young basidiomata, with a circular area surrounding the peristome. PERISTOME surface fibrillose, almost concolorous or somewhat darker than endoperidium, broadly conical to mammiform, distinctly delimited, 1–3.5 mm long. COLUMELLA cylindrical to club-shaped, slender, sometimes indistinct. MATURE GLEBA olivaceous brown to brown.

MYCELIAL LAYER consisting of dimorphic hyphae: (I) 2–4.5 μm thick, hyaline, thick-walled, rarely branched; (II) 2–3.5 μm thick, hyaline, thin-walled, with clamp-connections, branched. FIBROUS LAYER consisting of 3.5–7 μm thick, hyaline to pale yellowish brown, thick-walled hyphae. PSEUDOPARENCHYMATOUS LAYER consisting of thick-walled, hyaline, yellowish brown to reddish brown, almost bladder-like but variously shaped cells. ENDOPERIDIUM consisting of dimorphic hyphae: (I) 3.5–6 μm thick, hyaline to pale yellowish brown, thick-walled, rarely dichotomously branched; (II) 1.5–4.5 μm thick, hyaline to pale yellowish brown, thin-walled, branched. HYPHAE OF THE COLUMELLA 2–7 μm thick, thick-walled, surface smooth, hyaline to pale yellowish brown. HYPHAE OF THE CAPILLITIUM 2–6.5 μm thick, thick-walled, pale yellowish brown to yellowish brown, curved, tapered gradually towards subacute tips, rarely dichotomously branched, surface almost smooth or sometimes encrusted with amorphous remnants and crystalline materials. BASIDIA not seen. BASIDIOSPORES globose, densely verrucose, thick-walled, yellowish brown to olivaceous brown, 3.5–[4 $\pm$ 0.3]–4.5 μm diam. excluding ornaments, 4–[4.7 $\pm$ 0.4]–5.5 μm diam. including ornaments, verrucae conical to columnar-like, ≤ 0.7 μm high, with flat, rounded to subacute apices, basal apiculus prominent.

HABITAT AND DISTRIBUTION: Uncommon in Japan, solitary to gregarious on sand near *Carex kobomugi* and *C. pumila* in coastal dunes or on the ground in broad-leaved forests in a warm-temperate area. Fresh and old basidiomata were collected in July and December. Known from Japan (Shizuoka and Osaka, new record), China (Zhou et al. 2007), Europe (Hollós 1904, Sunhede 1989), South Africa (Bottomley 1948; Coetzee et al. 1997), North America (Coker & Couch 1928), Central America (Esqueda et al. 2003) and Hawaii (Gilbertson et al. 2001).

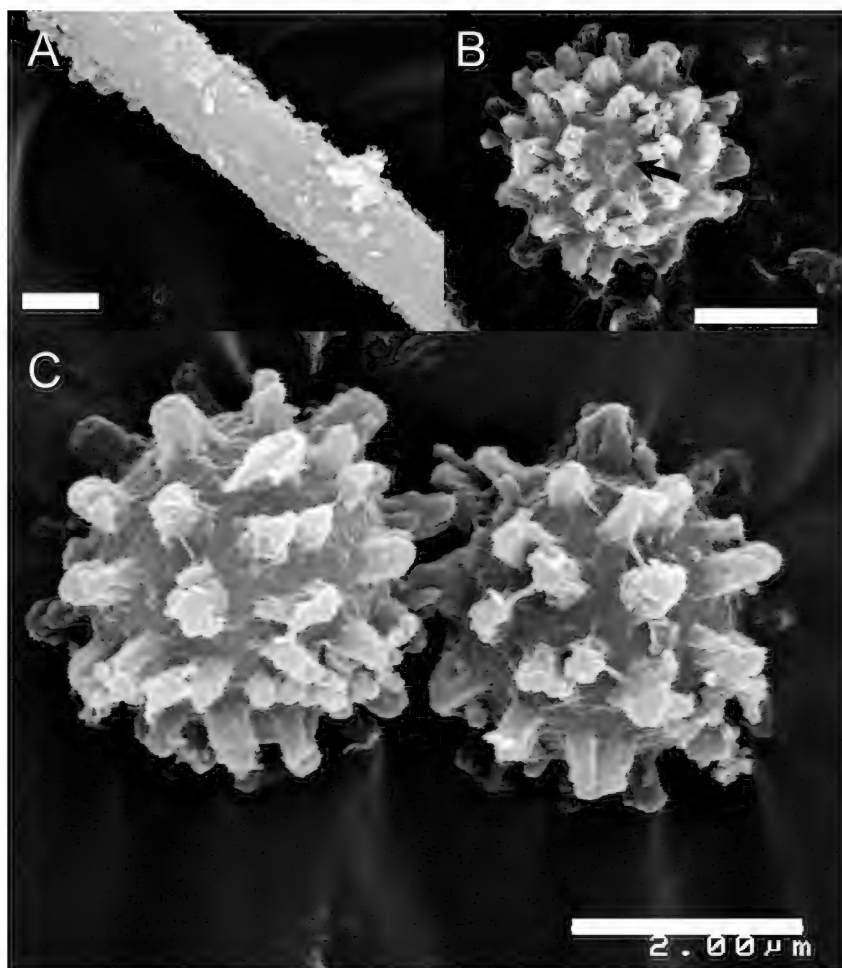


FIGURE 4. *Geastrum corollinum*: SEM micrographs (TNS-F-38711). A: Hypha of the capillitium encrusted with amorphous remnants and crystalline materials. B: A basidiospore with apiculus (arrow). C: Basidiospores with dense verrucae. Scale bars = 2 μ m.

SPECIMENS EXAMINED: JAPAN. SHIZUOKA PREFECTURE: Iwata-shi, Fukude: December 3, 2003, I. Asai, TNS-F-38711. OSAKA PREFECTURE: Katano-shi, Kaigake-no-michi: July 31, 2011, Y. Kotera, TNS-F-550009.

COMMENTS: *Geastrum corollinum* is diagnosed by hygroscopic exoperidial rays, a smooth mycelial layer not encrusted with sand or debris, and a distinctly delimited, fibrillose peristome. The morphology of the Japanese specimens

agrees well with previous descriptions of *G. corollinum* (Hollós 1904, Dissing & Lange 1962, Sunhede 1989). However, the pseudoparenchymatous layer of the exoperidium of the Japanese material is thinner (≤ 0.5 mm thick) than that of European material (0.5–1.5 mm thick, Sunhede 1989).

Gastrum floriforme Vittad. and *G. hungaricum* are morphologically similar to *G. corollinum*. However, *G. floriforme* basidiomata are hypogeous when unexpanded and have indistinctly delimited peristomes and the mycelial layer is encrusted with sand or plant debris (Sunhede 1989). For comparison with *G. hungaricum*, see description and comments below. *Gastrum arenarium* Lloyd, which resembles *G. corollinum* macroscopically, differs in its mycelial layer strongly encrusted with sand or plant debris (Sunhede 1989) and smaller basidiospores of *G. arenarium* (3.5–4.5 μm diam. including ornaments, Sunhede 1986).

Japanese specimens of *G. corollinum* have been collected from coastal sand dunes along the Pacific Ocean and under broad-leaved forests of warm-temperate areas of Central Honshu. In Europe, the type locality of *G. corollinum*, it has been obtained from various habitats, under deciduous trees (Dissing & Lange 1962, Sunhede 1989), under *Juniperus communis* (Sunhede 1989), and in sandy grasslands (Dörfelt et al. 1979) and coastal dunes (Eyndhoven 1937). Chinese specimens have been collected from grasslands, grazed fields and under *Cryptomeria japonica* or several salicaceous trees (Zhou et al. 2007). *Gastrum corollinum* has also been recorded from tropical deciduous forests in Mexico (Esqueda et al. 2003) and dry, coastal to montane forests in Hawaii (Gilbertson et al. 2001). Ecologically, these facts suggest that the present fungus adapts to varied environments. In Japan, further fieldwork is needed to clarify whether the distribution of *G. corollinum* is limited to coastal sand dunes or not.

Gastrum corollinum has been recorded from all continents except Antarctica. Given the variable morphological characters (Dissing & Lange 1962, Sunhede 1989) and diverse habitats, *G. corollinum* probably comprises a species complex.

Gastrum hungaricum Hollós, Math. Természettud. Értes. 19(5): 506, 1901,

as “*Geaster hungaricus*”.

FIGS. 5–6

JAPANESE NAME: Arechi-no-himetsuchiguri (dry wastelands earthstar, newly named here).

UNEXPANDED BASIDIOMATA hypogeous to subhypogeous, depressed globose, subglobose to ovoid, ca. 3–10 mm diam., surface encrusted with sand and plant debris, whitish to slightly cineraceous. EXPANDED BASIDIOMATA 5–12 mm across when dried, 13–17 mm across when wetted, exoperidium splitting into 6–11 rays, strongly hygroscopic, partly or entirely covering the endoperidial body when dried, tips of the rays sometimes become curved downwards in



FIGURE 5. *Geastrum hungaricum*: macrocharacters. A: An expanded basidioma (TNS-F-38713) with distinctly delimited, fibrillose peristome. B: Expanded basidiomata (TNS-F-38712) showing strongly hygroscopic exoperidial rays. Note basal remnants of the mycelial layer attached to basidiomata with sand and plant debris (arrows). C: An expanded basidioma (TNS-F-38713) in the natural habitat. Scale bars: A, C = 5 mm; B = 10 mm.

fresh state. MYCELIAL LAYER thin, whitish, with sand and plant debris, easily peeling off and usually forming basal remnants attached to the basidiomata. FIBROUS LAYER firmly, persistently attached to the pseudoparenchymatous layer, outer side white. PSEUDOPARENCHYMATOUS LAYER persistent, cream to pale beige in fresh state, later becoming pale brown, reddish brown to

dark brown. ENDOPERIDIAL BODY sessile, globose, subglobose to ovoid, 2–9 mm diam., without apophysis. ENDOPERIDIUM pale brown to greyish brown, almost smooth when old, but usually pruinose with whitish to beige crystalline material in fresh basidiomata, with a circular area surrounding the peristome. PERISTOME surface fibrillose, almost concolorous or somewhat darker than endoperidium, discoid to broadly conical, distinctly delimited, 0.5–1.5 mm long. COLUMELLA cylindrical, slender, sometimes indistinct. MATURE GLEBA olivaceous brown to brown.

MYCELIAL LAYER consisting of dimorphic hyphae: (I) 2–5.5 μm thick, hyaline, thick-walled, rarely branched; (II) 2–5 μm thick, hyaline, thin-walled, rarely with clamp-connections, sparsely branched. FIBROUS LAYER consisting of 3–7.5 μm thick, hyaline to pale yellowish brown, thick-walled hyphae. PSEUDOPARENCHYMATOUS LAYER consisting of thick-walled, hyaline to pale brown, almost bladder-like but variously shaped cells. ENDOPERIDIUM consisting of 2.5–5 μm thick, hyaline, pale yellowish brown to pale brown, thick-walled hyphae encrusted with amorphous crystalline materials. HYPHAE OF THE COLUMELLA 1–6 μm thick, thick-walled, surface smooth, pale yellowish brown. HYPHAE OF THE CAPILLITIUM 1–8 μm thick, thick-walled, pale yellowish brown to yellowish brown, tapered gradually towards subacute tips, sometimes dichotomously branched, surface almost smooth or encrusted with some amorphous remnants and crystalline materials. BASIDIA not seen. BASIDIOSPORES globose, warty, thick-walled, olivaceous brown to dark brown, 4.3–[4.9 $\pm$ 0.3]–5.3 μm diam. excluding ornaments, 4.8–[5.4 $\pm$ 0.3]–5.8 μm diam. including ornaments, warts radiating from the base of the apiculus and connecting to adjacent verrucae thus showing wing-like, $\leq$ 0.5 μm high, with rounded to subacute apices, basal apiculus prominent.

HABITAT AND DISTRIBUTION: Uncommon in Japan, gregarious or solitary on sand among mosses near *Elymus mollis* in coastal dunes in a cool-temperate area. One fresh basidioma was collected in September; several overwintered, old specimens were found in May. Known from Japan (Hokkaido, new record), Mongolia (Dörfelt & Otto 1985), Russian Karachay-Cherkessia (Hollós 1904), Hungary (Hollós 1904), Czech Republic (Staněk 1958), and Germany (Dörfelt et al. 1979).

SPECIMENS EXAMINED: JAPAN. HOKKAIDO: Shari-gun, Shari-cho, Minehama: May 29, 2009, T. Hoshino and A. Uchida, TNS-F-38712; September 27, 2010, A. Uchida, TNS-F-38713.

COMMENTS: *Geastrum hungaricum*, one of the smallest *Geastrum* species of the genus, is well characterized by strongly hygroscopic exoperidial rays, an endoperidium with a pruinose surface with whitish to beige crystalline material, and a distinctly delimited, fibrillose peristome. The morphology of the Japanese specimens agrees well with previous descriptions of *G. hungaricum* (Hollós

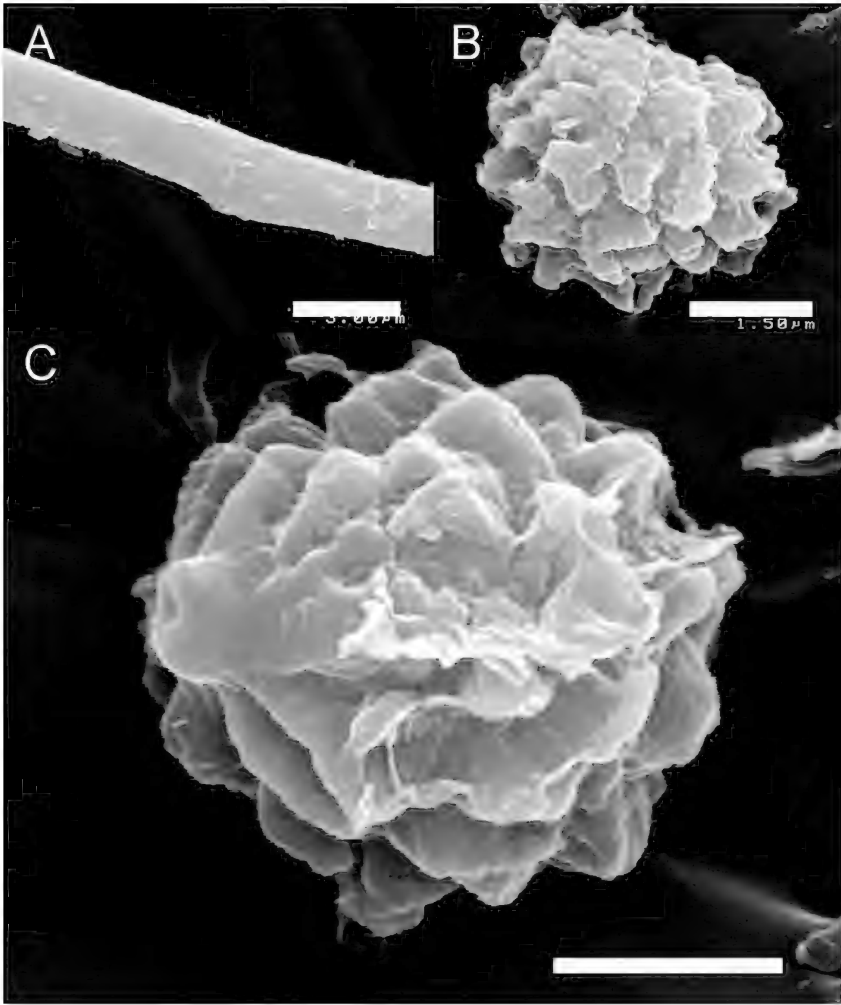


FIGURE 6. *Geastrum hungaricum*: SEM micrographs. A: Hypha of the capillitium sparsely encrusted with amorphous remnants and crystalline materials (TNS-F-38712). B: A basidiospore covered with dense verrucae (TNS-F-38712). C: A basidiospore with prominent apiculus (TNS-F-38713). Note wing-like verrucae radiating from the base of the apiculus. Scale bars: A = 3 µm; B–C = 1.5 µm.

1904, Staněk 1958, Sunhede 1989), except that the basidiospores are slightly narrower than in European materials (5–6 µm diam. including ornaments, Sunhede 1989).

Two other small-sized earthstars, *G. corollinum* and *G. floriforme*, resemble *G. hungaricum*. However, unexpanded basidiomata of *G. corollinum* are epigeous, onion-shaped with an umbo, with brownish surfaces, and not encrusted with sand or plant debris (Sunhede 1989; see also our description of *G. corollinum*, above) and the expanded basidiomata are larger (≤ 23 mm diam., Sunhede 1989). *Geastrum floriforme* clearly differs from *G. hungaricum* by its indistinctly delimited peristome, smooth endoperidial surfaces, and larger basidiospores (≤ 7 μ m diam., Sunhede 1989).

Japanese material of *G. hungaricum* was collected from a coastal sand dune along the Sea of Okhotsk in the cool-temperate area of eastern Hokkaido, while the type was collected from Hungary. In Europe it has been collected from sandy, rocky or grazed ground (Hollós 1904, Staněk 1958, Sunhede 1989), and Russian or Mongolian specimens were also found in semiarid areas (Hollós 1904, Dörfelt & Otto 1985), suggesting that *G. hungaricum* habitats are limited to dry, sandy, stony or grazed ground in northern cool-temperate regions.

Acknowledgments

We thank Mr. Ikuo Asai (Saitama, Japan), Dr. Tsuyoshi Hosoya (National Museum of Nature and Science, Japan) and Mr. Yuzo Kotera (Kyoto, Japan) for their collaborations and suggestions to our study. The authors are also grateful to Dr. Don Hemmes (University of Hawaii, U.S.A.) and to Dr. Vagner Gualarte Cortez (Universidade Federal do Paraná, Brazil) for their critical reviews of the manuscript. Thanks are also owed to Dr. Francisco D. Calonge (Madrid Botanical Garden, Spain) for his valuable comments on this study. This research was financed in part by a JSPS grant-in-aid (No.222635) to TK and a JSPS grant-in-aid for young scientists B (No. 21770096) to KH. This work is in partial fulfillment of the requirements for the Ph.D. degree of TK.

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